The temporal and spatial distribution of Triassic dinoflagellate cysts

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Abstract

The records of dinoflagellate cysts from the Late Triassic, the time during which they first appear abundantly in the geological record, are reviewed. Most of the Triassic palynological literature pertains to terrestrial palynomorphs, thus it is challenging to establish a global picture of the temporal and spatial distribution of Late Triassic dinoflagellate cyst around the supercontinent of Pangea. Moreover, data on Late Triassic dinoflagellate cysts are dispersed, and there are currently no records of dinoflagellate cysts from many marine successions. With the exception of an Australian record of the dinoflagellate cyst *Sahulidinium ottii* from the late Mid Triassic, and a possible early Carnian occurrence of, among others, *Rhaetogonyaulax* in the Swiss Alps, cyst-forming dinoflagellates first appeared relatively synchronously around Pangea from the late Carnian. There are three to six species of pre-Norian species globally, whereas species richness exceeded 25 by the end of the Norian. During the Rhaetian, marine seaways had gradually opened due to sustained continental breakup, allowing the expansion of dinoflagellates into many European basins. New species are present, some known only from restricted areas, whereas others like *Dapcodinium* appear to have a global distribution. The majority of Triassic dinoflagellate cyst taxa do not extend into the Jurassic.

Keywords

biostratigraphy; dinoflagellate cysts; geographical and temporal distributions; Triassic

1. Introduction

1.1. Background

Knowledge of the origination of cyst-forming dinoflagellates and their geographical and stratigraphical distribution around Pangea during the Late Triassic is relatively poor. These widely separated data, many from studies not principally focussed on dinoflagellate cysts, makes it difficult to obtain a comprehensive overview of their spatial and temporal distributions. Knowledge of the composition of the various Late Triassic assemblages varies due to a lack of quantitative data, and is therefore in part poorly known. Another complicating factor regarding their evolution includes the fact that the Late Triassic spans ~36 my (Lucas, 2010; Gradstein et al., 2012, Ogg et al. 2016) and the stratigraphical resolution is relatively poor, with a lack of macrofossil data and geochronological dating in most areas. In addition, many relevant publications are relatively old and have applied chrono- and lithostratigraphical nomenclature, which now is outdated, thereby hampering reliable age assignments and correlation. Determining exact stratigraphical occurrences and establishing correlations are therefore difficult, and age assignments of the dinoflagellate cyst records have, as a result, varying levels of uncertainty. Most of the ages given below are those from published studies and many of these have relatively large uncertainties in the ranges quoted. The relationships between the dinoflagellate cysts that evolved in northern Pangea and their counterparts from the southern margins of Neotethys are therefore unclear. To date, there are no records of Late

Triassic dinoflagellate cysts from intermediate regions such as the western or eastern margins of Pangea.

As dinoflagellate cysts are important for relative age dating and correlation, as well as proxies for some paleoenvironmental aspects, understanding their occurrence in time and space is valuable (Stover et al., 1996). The nature of the data, as outlined below, makes it challenging to establish an overview of Late Triassic dinoflagellate cyst distribution. A better understanding of their occurrences in time and space is therefore required. This overview and synopsis cannot provide comprehensive answers to all these questions. However, by providing a global overview and presenting the state of the art on dinoflagellate cyst distributions in space and time during the Late Triassic Epoch, we hope to provide a significantly improved understanding. This paper therefore seeks to review existing knowledge of the occurrences of Late Triassic dinoflagellate cysts along the coastlines of Pangea. Following a summary of the known dinoflagellate cyst records from the various geographical areas, their records and occurrences along the margins of Pangea are discussed, in a stratigraphical context with reference to the various geographical records. A short note on their paleoenvironmental significance is included. However to make further advances in this regard, more work is needed in areas with marine Upper Triassic successions.

1.2. Triassic dinoflagellate cysts, state-of-the-art

During the Late Triassic, landmasses were relatively symmetrically situated around the equator, forming Pangea (Figure 1). Along the margins of this supercontinent, marine deposition occurred. However, most Upper Triassic successions are terrestrial, having been deposited in various continental, siliciclastic depositional systems produced by continental rifting. During the Late Triassic, rifting increased, eventually leading to seafloor spreading and the breakup of Pangea (Ziegler et al., 1983, 2003; Golonka, 2004, 2007; Golonka et al., 2018). Consequently, marine deposition took place in some of these rifts, and the areal extent of marine borderlands increased.

Surrounding the Late Triassic continents, the first abundant cyst-forming dinoflagellates evolved, developed and spread into these relatively shallow marine environments. According to MacRae et al. (1996), about 24 species of dinoflagellate cysts had developed globally by the Norian. Dinoflagellate cysts continued to expand throughout the Jurassic to peak in diversity in the Cretaceous (MacRae et al., 1996). Dinoflagellates represent a substantial part of the phytoplankton population in the oceans today, and are one of the major primary producers (Wiggan et al., 2018). In the fossil record, dinoflagellate cysts represent valuable tools for biostratigraphy, palaeoclimatology and palaeoecology. This is despite the fact that only about 15 % of extant dinoflagellate species produce fossilisable cysts (Head, 1996).

Figure 1. The palaeogeography of the Late Triassic illustrating the locations of the first occurrences of dinoflagellate cyst records (adapted from Golonka et al. 2018).

The first appearance of fossil dinoflagellate cysts in the geological record has been extensively debated (Bujak and Williams, 1981; Fensome et al., 1999). Le Herisse et al. (2012) ruled out the presence of body fossils of dinoflagellate cysts older than the Triassic, but they are cytologically primitive and their phylogenetic lineages may be as old as the Precambrian (Evitt, 1985; Fensome et al., 1999). This is also indicated by biogeochemistry studies on dinosteranes (Moldowan et al. 1996, Moldowan & Talyzina 1998). The Australian peridiniphycidaen species *Sahulidinium ottii* is however the oldest known fossil dinoflagellate cyst (Harland et al., 1975; Stover and Helby, 1987). The reasons and circumstances leading to their appearance at this time is unclear. Falkowski et al. (2004a, b) suggested that changes in the ocean chemistry was a major factor. *Sahulidinium ottii* was described from the upper Middle Triassic (Ladinian) to lowermost Carnian of Australia (Helby et al. 1987a; Riding et al. 2010), however independent dating is lacking. Despite this isolated, probably uppermost Middle Triassic occurrence, on a global scale, dinoflagellate cysts first appeared and evolved with relatively low diversities during the Late Triassic (MacRae et al., 1996). Whether these represent the first significant evolutionary development of dinoflagellates, or cyst-forming dinoflagellates, or whether the longest lineages have developed over time is still not fully understood. Following *S. ottii* stratigraphically, the peridiniphycidaen genus *Rhaetogonyaulax* appears to be the first to emerge around the shores of Pangea during the Carnian (e.g. Riding et al., 2010, Vigran et al., 2014; Paterson and Mangerud, 2015).

On a global scale, Late Triassic palynological data are relatively extensive but mainly comprises records of terrestrially-derived palynomorphs. Several useful reviews on these terrestrial floras have been produced, including Helby et al. (1987a), Cirilli (2010), Kürschner and Herngreen (2010), Césari and Colombi (2013) and Li et al. (2016). In addition, papers on the Triassic-Jurassic (Tr–J) boundary provide important contributions on dinoflagellate cyst occurrences (see e.g. Lindström 2016). Despite the early pioneer work on Late Triassic palynology, including dinoflagellate cysts from the present high Arctic (Wiggins, 1973; Fisher and Bujak, 1975; Bujak and Fisher, 1976), relatively little work has been undertaken on this region since. Recent work on Late Triassic palynology in the Barents Sea area has, however, revealed several records of dinoflagellate cysts (Vigran et al., 2014).

Late Triassic dinoflagellate cysts have been extensively recorded, but many papers in which reports are present are principally focussed on the biostratigraphy of terrestrial palynomorphs (e.g. Morbey and Neves, 1974; Smith, 1974; Warrington, 1974; Felix, 1975; Bjærke and Manum, 1977; Warrington, 1978; Suneby and Hills, 1988; Aghanabati et al., 2002, 2004; Warrington, 2005; Paterson and Mangerud, 2015, Vigran et al., 2014). In addition, papers on the Triassic–Jurassic boundary (e.g. Warrington, 1983; Mettraux and Mohr, 1989; Embry and Suneby, 1994; Warrington et al., 1995; Lindström and Erlström, 2006; Kürschner et al., 2007; Bonis et al., 2009; Ruckwied and Götz, 2009) and papers on sequence stratigraphy (e.g. Paterson et al., 2016; Lindström et al., 2017b) have recorded Late Triassic dinoflagellate cysts. The recorded genera include the suessiaceans *Beaumontella, Lunnomidinium, Noricysta, Suessia* and *Wanneria,* together with the peridiniphycidaen forms *Dapcodinium, Hebecysta*, *Heibergella, Rhaetogonyaulax*, *Sahulidinium, Sverdrupiella* and *Valvaeodinium* (Table 1). The composition of these Late Triassic assemblages varies, and is often poorly known in part due to a lack of quantitative data. Another complicating factor regarding their evolution includes the fact that the Late Triassic spans ~36 myr (Lucas, 2010; Gradstein et al., 2012, Ogg et al. 2016), and the stratigraphical resolution is relatively poor, with a lack of macrofossil data and geochronological dating in many areas. Determining exact stratigraphical occurrences and establishing correlations are therefore difficult, and age assignments of the dinoflagellate cyst records have, as a result, varying levels of uncertainty.

TABLE 1. List of dinoflagellate cyst taxa appearing in Upper Triassic successions. References to the author citations can be found in Williams et al. (2017).

Most of the ages given in section 3 below, are taken from published studies, and as few independent age controls are available, there are relatively large uncertainties in the ranges quoted (Figure 2). This paper summarises all published Late Triassic dinoflagellate cyst occurrences, followed by a review of their stratigraphical importance and geographical extent along the margins of Pangea.

2. Records of Late Triassic dinoflagellate cysts from various regions

2.1. The present Arctic

During the Late Triassic, large volumes of siliciclastic sediment were deposited along the northern margins of Pangea. These now comprises the offshore and onshore successions of the North Slope of Alaska, the Sverdrup Basin in the Canadian Arctic, Svalbard in the Norwegian Arctic, the Barents Sea spanning the Norwegian-Russian sector and various basins along the northern margins of Russia. Transgressive–regressive cycles have been confidently correlated throughout this vast area (Mørk et al., 1989; Embry, 1997; Egorov and Mørk, 2000; Mørk and Smelror, 2001), partially well dated by ammonites (e.g. Dagys et al. 1993).

Terrestrially derived material, mainly pollen and spores, dominate palynofloras from the Upper Triassic successions of the present Arctic (e.g. Suneby and Hills, 1988; Hochuli et al., 1989; Ilyina and Egorov, 2008; Vigran et al., 2014). However, marine palynomorphs are relatively common in parts of these successions (e.g. Felix and Burbridge, 1978; Hochuli et al., 1989; Vigran et al., 2014) and provide valuable information, for example on palaeoecology. These marine assemblages mainly comprise acritarchs, largely the spine-bearing genera *Micrhystridium* and *Veryhachium*, but also include levels dominated by dinoflagellate cysts.

2.1.1. The Norwegian Arctic (the Barents Sea area including Svalbard)

During the Triassic, the Barents Sea (including Svalbard) was an intracratonic basin, situated within a large embayment that had developed during the Late Palaeozoic (Worsley, 2008). During the Late Triassic, most of this embayment was filled by vast quantities of sediment sourced from the eastern and south-western margins of the basin. Triassic rocks extensively outcrop in the Svalbard Archipelago, and thick deposits are widely distributed in the subsurface of the Barents Sea (Mørk et al., 1982; Rønnevik et al., 1982; Faleide et al., 1984; Mørk et al., 1993; van Veen et al., 1993; Riis et al., 2008). Palynological studies of the Late Triassic which reported dinoflagellate cysts include Smith et al. (1975), Bjærke (1977), Bjærke and Dypvik (1977), Bjærke and Manum (1977), Hochuli et al. (1989), Nagy et al. (2011), Mueller et al. (2014), Vigran et al. (2014), Paterson and Mangerud (2015, 2017) and Paterson et al. (2016, 2018. No records of dinoflagellate cysts below the Kapp Toscana Group have been observed, with the exception of questionable *Sentusidinium*-like cysts recovered from the Botneheia Formation at one locality in Spitsbergen (Vigran et al., 2014, pl. 5).

Records of dinoflagellate cysts from the Island of Hopen (Smith et al., 1975; Bjærke and Manum, 1977; Vigran et al., 2014; Paterson and Mangerud, 2015; Paterson et al., 2016) are based on material from the lower and middle Flatsalen Formation, which is assigned an early Norian age based on ammonites (Korčinskaya, 1980; Smith, 1982). A dinoflagellate cyst assemblage, which is dominated by *Rhaetogonyaulax rhaetica,* is recorded in this unit (Paterson and Mangerud, 2015). *Rhaetogonyaulax rhaetica* is also recorded from the underlying De Geerdalen Formation (Middle to Upper Carnian) in very low proportions. Although devoid of age diagnostic macrofossil, the age of the Geerdalen Formation is well constrained (Paterson & Mangerud 2015, page 103–104).

On Spitsbergen, the oldest records of dinoflagellate cysts are from the Isfjorden Member of the De Geerdalen Formation (Upper Carnian) and in the Knorringfjellet/Flatsalen formations (Norian). Occurences from the De Geerdalen Formation are largely sporadic and rare, and are mainly confined to the upper part. However, at one locality (Festningen), they sporadically occur in high abundances. At the same locality in the Knorringfjellet Formation (Norian), the dominant species is still *Rhaetogonyaulax rhaetica*, but often *Heibergella* and *Sverdrupiella* are also present (Vigran et al., 2014). This association was also observed at Wilhelmøya Island in eastern Svalbard (Vigran et al., 2014). A rich assemblage of *Rhaetogonyaulax*, including *Rhaetogonyaulax rhaetica,* together with *Sverdrupiella,* was also recorded from the Flatsalen Formation of a Sentralbanken core (7533/2-U-2) in the central Barents Sea (Vigran et al., 2014; Paterson et al., 2018). The latter study concluded that the records of dinoflagellate cysts in the overlying Norian–Rhaetian Svenskøya Formation observed in core 7532/2-U-1 by Vigran et al. (2014) are not *in situ*, as they are in an interval with extensive rip-up clasts and are interpreted as reworking.

In the southern Barents Sea, Vigran et al. (2014) and Paterson and Mangerud (2017) recorded low numbers of *Rhaetogonyaulax rhaetica* in Norian strata from exploration wells, coeval with the Hopen successions. A few species of *Noricysta* and *Sverdrupiella* were also found in an offshore well in strata of presumed Norian age by Vigran et al. (2014). In the few Upper Triassic successions dominated by acritarchs from exploration wells in the southern Barents Sea area, dinoflagellate cysts are however rare. This probably indicates a proximal, paralic environment with minor marine incursions, where the early Norian transgression barely reached the southern margins of the basin (Bugge et al., 2002; Glørstad-Clark et al., 2010; Klausen et al., 2015).

2.1.2. The Sverdrup Basin, Canadian Arctic

Further west in the huge embayment which includes the Barents Sea area, the Sverdrup Basin was an active depocentre between the Early Carboniferous (Mississippian) and the Neogene. During the Late Triassic, this large rift/sag basin gradually subsided and was mainly filled by deltaic deposits from the south and southwest. During the Norian, it also received sediments from “Crockerland” to the north (Embry, 2009, 2011).

The palynology of early exploration wells in the Sverdrup Basin, where Upper Triassic rocks are extensively exposed, has been investigated. This pioneering work on Late Triassic dinoflagellate cysts from the Triassic part of the Heiberg Formation proved highly significant. Macrofossil data are present but scarce, indicating a Norian age (Suneby and Hills

1988, p. 348). The dinoflagellate cyst assemblages were described to various degrees in a number of papers including Brideaux (1975), Felix (1975), Fisher and Bujak (1975), Bujak and Fisher (1976), Souaya (1976), Felix and Burbridge (1978), Staplin 1978 and Fisher and van Helden (1979). Suneby and Hills 1988 established the first palynological zonation for this unit based on a quantitative palynological approach for the Heiberg Formation. Embry and Suneby (1994) later focused primarily on the palynology of the Triassic–Jurassic boundary.

Fisher and Bujak (1975) and Bujak and Fisher (1976) worked on material from eight wells from the western Queen Elizabeth Islands in the western Sverdrup Basin. Bujak and Fisher (1976) described four new genera from the lower Heiberg Formation: *Sverdrupiella*, with eleven new species (nine of which are still valid); *Heibergella* and *Noricysta*, with three new species each; and *Hebecysta*, as a monotypic genus (*Hebecysta brevicornuta*). The samples were rich in the species *Sverdrupiella mutabilis*, *Sverdrupiella sabinensis, Sverdrupiella septentrionalis* (including *Sverdrupiella cristata* and *Sverdrupiella downeii)* and *Sverdrupiella usitata*. *Heibergella* was also relatively common, with *Heibergella asymmetrica* being the most common species of this genus. The other species were sporadic and rarer. *Noricysta fimbriata, Noricysta pannucea* and *Noricysta varivallata* were largely recorded only from one sample in the Sandy Point L-46 well. Several of the new species of *Sverdrupiella,* including *Sverdrupiella baccata, Sverdrupiella manicata, Sverdrupiella ornaticingulata, Sverdrupiella raiaformis* and *Sverdrupiella spinosa,* have never been reported from elsewhere. *Rhaetogonyaulax* was reported as being extremely rare and was only present in two cuttings samples (Bujak and Fisher 1976). However, according to Fisher and Bujak (1975), it is persistently present. Fisher and van Helden (1979) later stated, of *Rhaetogonyaulax:* “Representatives of the genus are often abundant in Late Triassic sediments from the Arctic Islands”. They noted the resemblance to *Rhaetogonyaulax rhaetica* from the Rhaetian of England. Their three new species (*Rhaetogonyaulax testacea,* *Rhaetogonyaulax tortuosa* and *Rhaetogonyaulax uncinata*) were later reclassified as a junior synonym of *Rhaetogonyaulax rhaetica* (Below, 1987a,b).

Felix and Burbridge (1977, 1978) reported abundant *Sverdrupiella usitata* from offshore exploration wells, but not from equivalent successions onshore. They also recorded *Hebecysta brevicornuta*, *Heibergella asymmetrica*, *Noricysta fimbriata*, *Rhaetogonyaulax arctica* (as *Shublikodinium arcticum*) and *Rhaetogonyaulax rhaetica.* Felix and Burbridge (1977, 1978) also noted that *Rhaetogonyaulax arctica* is present abundantly in the Schei Point Group, underlying the Heiberg Formation. The upper part of their Schei Point Group is now the Barrow Member of the Heiberg Formation. Those authors implied a Norian age for these assemblages based on palynological correlation, but did not exclude the possibility that they range down into the Carnian. The only record of dinoflagellate cysts below the Barrow Member is *Rhaetogonyaulax arctica*. In contrast to the species listed above, Felix (1975) reported common *Rhaetogonyaulax rhaetica* in the Heiberg Formation from nearby Ellef Ringnes Island, however, no quantitative data were provided.

Suneby and Hills (1988) erected the first palynological zonation of the Heiberg Formation and the uppermost Barrow Formation based on outcrop samples. They reported rich assemblages of terrestrial palynomorphs and dinoflagellate cysts from outcrops on Ellesmere Island from the eastern Sverdrup Basin. Four palynozones were established, three of which are Late Triassic. The oldest one (the *Triancoraesporites ancorae*–*Camarozonosporites laevigatus* Biozone) was subdivided into two subzones. The youngest of these was characterised by the first appearance of the dinoflagellate cysts *Hebecysta brevicornuta, Heibergella aculeata*, *Heibergella asymmetrica, Noricysta fimbriata, Noricysta pannucea, Sverdrupiella mutabilis, Sverdrupiella sabinensis* and *Sverdrupiella usitata*. The subzones were assigned a Norian age based on an ammonite and bivalves (Norford et al., 1973; Embry, 1982). At McKinley Bay, near the basin margin, this subzone was only recognised in two closely spaced samples, indicating facies control of these assemblages. A few dinoflagellate cysts were also recorded from two localities in a narrow interval within the underlying subzone; including *Valvaeodinium* (as *Comparodinium*), *Rhaetogonyaulax* sp. cf. *R. dilatata* and *Suessia* sp. cf. *S. swabiana.* This subzone was tentatively assigned to the early to late middle Norian.

2.1.3. Alaska

During the Late Triassic, Alaska was situated on the northern shores of Pangea, probably facing the open Panthalassa Ocean (Figure 1). Triassic marine, sedimentary rocks of the Shublik Formation were deposited on a shallow shelf that was believed to be an upwelling zone, but this interpretation is not universally accepted (Parrish et al., 2001; Embry et al., 2002). The Shublik Formation outcrops across most of the northern front of the Brooks Range, extending into the North Slope subsurface and gradually pinching out into its distal equivalent, the Otuk Formation (Kelly et al., 2007). Independent evidence for the Shublik and Otuk formations being Late Triassic in age is the occurrence of the bivalve genus *Monotis* (Helby et al. 1987b). Despite extensive exploration of these units, very few palynological data on the Shublik and Otuk formations have been published.

The first published Late Triassic dinoflagellate record from this region was the pioneering work of Wiggins (1973) on core material from an exploration well in the Shublik Formation on the Alaskan North Slope. This work focused on taxonomy, describing 10 new species of *Shublikodinium*; this genus was reclassified and included in *Rhaetogonyaulax* (see Stover and Evitt, 1978; Lentin and Williams, 1989). *Shublikodinium* was split too broadly at the species level by Wiggins (1973), and Stover and Evitt (1978) simplified the 10 species into two, *Rhaetogonyaulax arctica* and *Rhaetogonyaulax dilatata.* Wiggins (1973) also briefly mentioned the occurrence of undescribed dinoflagellate cysts in his material. Later, Helby et al. (1987b) referred to *Sverdrupiella* occurrences from the middle to late Norian of the Shublik Formation in Alaska. The dinoflagellate cysts were recorded from layers with two different species of the bivalve *Monotis.*

In an open file report, Witmer et al. (1981) mentioned three Upper Triassic dinoflagellate zones and the occurrence of foraminifera. These authors listed dinoflagellate cysts including *Hebecysta* spp., *Noricysta* spp., *Suessia swabiana* and *Sverdrupiella* spp. Most of the studied wells were barren or had only rare dinoflagellate cyst occurrences; and the few specimens recorded were very poorly preserved.

Figure 2. A composite range chart of Late Triassic dinoflagellate cysts from various geographical areas (Time Scale from Gradstein et al. 2016).

2.1.4. Arctic Russia

Interestingly, despite the existence of ammonite-dated, fossiliferous marine successions from East Siberia (Russian Arctic) (Dagys et al., 1993, Egorov and Mørk, 1998; Konstantinov et al., 2003; Ilyina and Egorov, 2008), there are no published records of Late Triassic dinoflagellate cysts. However, *Rhaetogonyaulax* is present in Upper Triassic successions in the Anabar region, Northern Siberia (personal communication, Vera Pospelova 2018). We attribute the lack of published records of Late Triassic dinoflagellate cysts from this region to previous studies focussing exclusively on terrestrial palynomorphs.

2.2. Europe

The breakup of Pangea began during the Norian in the Late Triassic, and included the opening of parts of the western Tethys (Hauser et al., 2002). However, in southern Europe, the first rifting phases started in the Early Triassic, and carbonate platforms developed in the Calcareous Alps and the Inner Carpathians (Ciarapica, 2007; Golonka, 2007; Golonka et al., 2018). Many of the classic European Upper Triassic (Keuper) successions were non-marine. By contrast, during the Rhaetian, the incursion of intercontinental seaways into central Pangea caused the marine inundation of central Europe (Manspeizer, 1994, Hesselbo, 2012). Consequently, dinoflagellate cysts are absent in most pre-Rhaetian strata, although marine deposition took place earlier for example along the Neotethyan margins. The fact that there are very few records pre-dating the Rhaetian could be due to the poor preservation potential of the Neotethyan carbonate platforms and subsequent Alpine metamorphism may have also been influential.

Records of pre-Rhaetian dinoflagellate cysts in Europe include Hochuli and Frank (2000) from the Lower Carnian (Julian) marine dolomites of the Lower Raibl Group successions in eastern Switzerland in the Swiss Alps. These authors recorded indeterminate dinoflagellate cysts, cf. *Noricysta fimbriata,* cf. *Noricysta pannucea* and *Rhaetogonyaulax* cf. *wigginsii*. Hochuli and Frank (2000, 2006) made a correlation based on pollen and spores to the Lower Carnian (Julian) Stuttgart Formation of Germany; these are the oldest low latitude pre-Rhaetian dinoflagellate cysts. Heunisch (1986), however, reported acritarchs, but no dinoflagellate cysts, from the Carnian of Germany. A recent PhD thesis reported *Heibergella* sp. and indeterminate dinoflagellate cysts from boreholes in the Carnian Veszprém Marl Formation in the Transdanubian Range in Hungary (Baranyi 2018). By contrast, Götz et al. (2009) found that apparently marine Triassic–Jurassic boundary successions in Hungary are devoid of dinoflagellate cysts. Mettraux and Mohr (1989) reported *Rhaetogonyaulax rhaetica* from the Rhaetian of western Switzerland; *Dapcodinium priscum* was also observed in the uppermost strata close to the Triassic–Jurassic boundary. Similarly, Schneebeli-Hermann et al. (2018) recorded *Dapcodinium priscum*, *Rhaetogonyaulax rhaetica* and *Valvaeodinium* spp. from the Rhaetian of northern Switzerland.

Several authors have reported dinoflagellate cysts from Upper Triassic and Lower Jurassic Tethyan marginal shelf facies in Austria. Karle (1984) reported common *Rhaetogonyaulax rhaetica* from the upper Rhaetian mergel-facies in the Calcareous Austrian Alps. From the Kendelbachgraben in Austria, Morbey and Neves (1974) reported *Rhaetogonyaulax rhaetica* from the lowermost Rhaetian, and *Dapcodinium* and *Heibergella* (as *Rhombodella*) in overlying Rhaetian strata. Morbey (1975) published a major, pioneering biostratigraphical and taxonomic study. He described *Beaumontella caminuspina* (as *Cleistosphaeridium mojsisovicsii*), *Heibergella kendelbachia* (as *Rhombodella kendelbachia)*, *Suessia swabiana* and *Valvaeodinium koessenium* (as *Comparodinium koessenium*). Morbey (1975) also reported *Dapcodinium priscum* and *R. rhaetica* from the Rhaetian. Hoelstein (2004) recorded *Beamontella langii, Rhaetogonyaulax rhaetica*, *Suessia swabiana*, *Valvaeodinium koessenium* and *Wanneria listeri* from the Kössen beds of Austria. He demonstrated that the dinoflagellate cyst assemblages varied markedly in abundance throughout the successions. Important multidisciplinary contributions from this region include Krystin et al. (2007), Kürschner et al. (2007) and Bonis et al. (2009). Kürschner et al. (2007) integrated quantitative palynological data from the Tiefengraben with independent dating methods and clearly demonstrated the change from abundant *Rhaetogonyaulax rhaetica* to *Dapcodinium priscum* immediately below the Triassic–Jurassic boundary. Note the assemblage composition changed within the acme of *Dapcodinium priscum*, including the inception of *Beaumontella caminuspina* (as *Cleistosphaeridium mojsisovicsii*), *Beaumontella langii* and *Valvaeodinium koessenium*.

From the Tatra Mountains of Slovakia, Ruckwied and Götz (2009) reported rare to common occurrences of *Rhaetogonyaulax rhaetica* in a Triassic–Jurassic boundary section which is dominated by pollen and spores and calibrated by conodonts and foraminifera. This region was situated in an embayment of the Tethyan shelf at this time (Golonka, 2004), and *Rhaetogonyaulax rhaetica* was also recorded, although less frequently, in the lowermost Hettangian. Ruckwied and Götz (2009) observed rare *Dapcodinium priscum* from the Upper Rhaetian, with a more continuous record in the Hettangian. Michalík et al. (2010) also reported *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* from this area but stressed that marine palynomorphs are rare, attesting to shallow marine conditions. From the nearby Pieniny Klippen Belt in the West Carpathian of Poland, reworked *Rhaetogonyaulax rhaetica* was recorded and illustrated from Middle Jurassic successions by Gedl (2008) and Barski et al. (2012).

Upper Triassic strata from a borehole in Western Ciscaucasia, southern Russia, in the eastern Paleotethys, was studied by Yaroshenko (2007). *Dapcodinium priscum* and *Rhaetogonyaulax* were recorded, together with pollen and spores that are believed to be Rhaetian. However, this correlation is somewhat uncertain and the palynomorph assemblages could be as old as Norian.

The records of Late Triassic dinoflagellate cysts from the UK are all confined to the Rhaetian, and were eustatically controlled. The first record of Late Triassic dinoflagellate cysts was from Gloucestershire, southwest England (Sarjeant, 1963). Subsequently, Rhaetian dinoflagellate cyst assemblages from onshore and offshore UK, have been extensively reported by, for example, Warrington (1974, 1977a, 1977b, 1978, 1983, 1997, 2005), Warrington et al. (1986, 1995) and Bucefalo Palliani and Buratti (2006). Although the primary focus was on the rich terrestrially derived floras, Warrington (1974) first recognised the stratigraphical importance of *Dapcodinium priscum* and *Rhaetogonyaulax* in the Rhaetian of Lancashire, northwest England. Later, Warrington (1997, 2005) reported other dinoflagellate cysts, such as *Beaumontella caminuspina, Beaumontella langii* and *Valvaeodinium koessenium* from England.

Bucefalo Palliani and Buratti (2006) studied the Rhaetian of St Audrie's Bay and Manor Farm in southwest England. They recorded rich dinoflagellate cyst assemblages dominated by *Rhaetogonyaulax rhaetica* from the uppermost Mercia Mudstone and the Penarth groups. In addition, frequent *Suessia* sp. A from the Blue Anchor Formation and common *Dapcodinum priscum* from the uppermost Cotham Member (Lilstock Formation) were observed. Rare records of other species, including some not previously recorded in the UK, included *Heibergella asymmetrica*, *Heibergella* sp. cf. *H. salebrosacea, Noricysta pannucea, Suessia swabiana* and *Sverdrupiella mutabilis*. Bucefalo Palliani and Buratti (2006) presented semi-quantitative data, related their dinoflagellate cyst record to the palaeogeography and postulated migration events. These authors proved that dinoflagellate cysts were relatively diverse and rich by the Late Rhaetian in the UK.

Records of Rhaetian dinoflagellate cysts from Denmark and southern Sweden include Dybkjær (1988, 1991), Batten et al. (1994), Lindström (2002), Nielsen (2003), Lindström and Erlström (2006, 2007), Petersen et al. (2013) and Lindström et al. (2017a). An inverse quantitative relationship between *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* was noted by Batten et al. (1994), suggesting a relationship between brackish and marine environments.

Lindström (2002) described *Lunnomidinium scaniense* from the Rhaetian Höganäs Formation of southern Sweden from a succession dominated by pollen and spores. ?*Beaumontella caminuspina, Dapcodinium priscum, Rhaetogonyaulax rhaetica* and *Rhaetogonyaulax* sp. were also present sporadically. The evolution of *Lunnomidinium scaniense* and *Suessia* sp. A and their affinities to the Suessiaceae was discussed by Lindström (2006); these two forms may reflect different salinity levels. Only one occurrence of *Lunnomidinium scaniense* from Schandelach, Germany has been reported outside Sweden (Lindström et al., 2017b). Lindström and Erlström (2006b) related the occurrences of dinoflagellate cysts to a regional model and demonstrated that the acme of *R. rhaetica* corresponds to a Late Rhaetian maximum flooding event in the Danish Basin. Recently, Lindström et al. (2017a) researched the correlation of Triassic–Jurassic boundary successions with focus on the terrestrial ecosystems, but reported the dinoflagellate cysts ?*Beaumontella caminuspina, Lunnomidinium scaniense*, *Rhaetogonyaulax rhaetica, Suessia swabiana* and *Suessia* sp. A. They confirmed that *Rhaetogonyaulax rhaetica* is a regional marker for maximum flooding surfaces. Lindström et al. (2017b) also correlated Triassic–Jurassic boundary sections from northwest Europe, Nevada and Peru and demonstrated how various abundance events of *Rhaetogonyaulax rhaetica* can be applied in correlation.

In western Tethys, large areas of clay-rich sediments deposited in low dysoxic–anoxic basins have yielded dinoflagellate cysts from marine Rhaetian successions. This includes Sicily and southern Italy, where Cirilli et al. (2015) reported *Dapcodinium priscum* from the Rhaetian part of the Streppenosa Formation.

Several studies recorded Rhaetian dinoflagellate cysts from south-eastern France (Doubinger and Adloff, 1977; Adloff and Doubinger, 1982; Fauconnier et al., 1996; Courtinat et al., 1998; 2002; Courtinat and Piriou, 2002). Courtinat et al. (1998) reported rich assemblages from the Rhaetian near Lyon, including dominant *Rhaetogonyaulax rhaetica*, representing up to 95% of the palynomorphs. However, some horizons lack *Rhaetogonyaulax rhaetica*; in addition *Beaumontella caminuspina*, *Beaumontella delicata*, *Beaumontella langii, Dapcodinium priscum* and *Suessia swabiana* were observed. These authors interpreted the succession as representing a marginal marine setting, becoming fully marine up-section. *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* were observed in the largely paralic Rhaetian of the Massif-Central, south of Lyon by Courtinat et al. (2002) in a study otherwise focused on palynofacies from these paralic successions. From the same successions, Courtinat and Piriou (2002) discussed the changing quantitative occurrences in twelve Rhaetian sections of *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* and concluded that *Dapcodinium priscum* seemed to be an opportunistic species occupying specific ecological niches, whereas *Rhaetogonyaulax rhaetica* was a more open marine species.

2.3. Iran

Several publications have documented dinoflagellate cysts from the Upper Triassic of Iran including Aghanabati et al. (2002, 2004). The latter reported a relatively diverse assemblage including *Heibergella aculeata*, *Heibergella asymmetrica, Hebecysta balmei* and *Rhaetogonyaulax rhaetica*; this was divided into four assemblage zones, all of which are of inferred Norian age.

Ghasemi-Nejad et al. (2004) published on the Alborz Mountains, immediately south of the Caspian Sea. The dinoflagellate cysts were placed into the *R. wigginsii* and *R. rhaetica* zones of the *Rhaetogonyaulax* Superzone of the well-established Australian zonation. Independent ammonite dating suggests an early–middle Norian age for the *R. wigginsii* zone, which comprises abundant *R. wigginsii* and intervals of abundant *Heibergella aculeata, Heibergella asymmetrica* and *Heibergella salebrosacea*. By contrast, the *Rhaetogonyaulax rhaetica* zone is characterised by a monospecific assemblage of the index taxon.

From northeastern Iran, in a region which faced the Paleotethys, Ghasemi-Nejad et al. (2008) recorded diverse, poorly preserved Norian dinoflagellate cyst assemblages from the Miankuhi Formation. These included various species of *Hebecysta*, *Heibergella*, *Rhaetogonyaulax* and *Sverdrupiella* in addition to two indeterminate genera. Notably, *Rhaetogonyaulax rhaetica* was not recorded. Their age determination is based on correlation to the Upper Norian *H. balmei* zone of Australia.

Recent work in east-central Iran (Sabbaghiyan et al., 2015) described a rich dinoflagellate cyst assemblage from the Nayband Formation. This unit is Rhaetian in age based on plant macrofossils. *Rhaetogonyaulax rhaetica* is present throughout the interval studied however; *Dapcodinium priscum*, *Hebecysta brevicornuta Heibergella asymmetrica*, *Heibergella kendelbachia*, *Heibergella salebrosacea*, *Noricysta pannucea* and *Sverdrupiella* cf. *mutabilis* are also present.

2.4. Oceania

Upper Triassic successions mainly comprising deltaic, estuarine and marginal marine successions have been extensively studied throughout the North West Shelf of Australia and many wells have provided an extensive palynomorph database (Figure 2). Palynology, and in rare cases conodonts, are the only biostratigraphical tools used, and the palynomorph assemblages are largely dominated by pollen and spores. However, some contributions include reports of dinoflagellate cysts (Helby et al., 1987a; Brenner, 1992; Nicoll and Foster, 1994; Backhouse and Balme, 2002; Backhouse et al., 2002).

The first Mesozoic palynomorph biozonation of the North West Shelf of Australia was by Helby et al. (1987a), and was based on both marine and terrestrially derived forms. These authors defined the *Shublikodinium* (now *Rhaetogonyaulax*) middle Triassic to lower Jurassic Superzone which is of Anisian–Pliensbachian age. This unit includes six dinoflagellate cyst zones, the oldest is based on the occurrence of *Sahulidinium ottii* in the Sahul Shoals-1 well. In ascending order, their zones were based on the lowest occurrence of *Rhaetogonyaulax wigginsii*, *Suessia listeria* (now *Wanneria listeri*), *Hebecysta balmei* and *Rhaetogonyaulax rhaetica*. The youngest zone (within the Superzone) is the *Dapcodinium priscum* zone (as the *Dapcodinium priscus* Zone) which has a base in the uppermost Rhaetian is defined by the total range of *Dapcodinium priscum*.

Riding et al. (2010) critically reviewed the chronostratigraphical ages of the zones of the *Rhaetogonyaulax* Superzone of Australia. The age of the base of this unit was revised to Late Ladinian, probably Carnian, as opposed to Anisian. Furthermore, the base of the *Rhaetogonyaulax wigginsii* zone was considered to be latest Carnian, and the uppermost occurrence of *Rhaetogonyaulax rhaetica* is in the latest Triassic. According to Riding et al. (2010) there is then a hiatus spanning most of the Carnian placing the base of the overlying *Rhaetogonyaulax wigginsii* Interval Zone in the latest Carnian ranging up to the Middle Norian. This is in contrast to Helby et al. (1987) who placed the base of the *Rhaetogonyaulax wigginsii* zone near the base of the upper Carnian and its top at the base of the Norian (Riding et al. 2010, fig. 3). At present most Australian palynologists align with Helby et al. (1987) (personal communication, Daniel Mantle 2018).

Riding et al. (2010) also commented that of the 11 Triassic dinoflagellate cyst taxa in the *Rhaetogonyaulax* Superzone, six are known from Europe, whereas the other five (*Hebecysta balmei*, *Rhaetogonyaulax wigginsii*, *Sahulidinium ottii*, *Suessia* sp. A and *Wanneria listeri*) are only known from Australia. However, *Wanneria listeri* had been recorded from Austria by Feist-Burkhardt et al. (2002).

The work of Brenner (1992) was from Ocean Drilling Program material drilled on the Wombat Plateau off northwest Australia and includes records of *Hebecysta balmei* (as *Heibergella balmei)*, *Wanneria listeri* (as *Suessia listeria*), *Suessia swabiana* and *Rhaetogonyaulax rhaetica*. He also provided plates of various unidentified and undescribed forms, including species of *Noricysta*?, *Suessia* and *Rhaetogonyaulax*.

The first report of Late Triassic dinoflagellate cysts from New Zealand was a study of the upper Norian by Wilson and Helby (1986) from the southern island. Subsequently, Helby and Wilson (1988) described *Sverdrupiella warepaensis* from the type section of the Warepan Stage, Otago. They reported *Sverdrupiella* to be the predominant dinoflagellate genus occurring in association with only one single specimen of *Rhaetogonyaulax*. The assemblage is recorded in beds with *Monotis* shellbeds which correlates to the Cordillaranus Zone of late Norian age.

Martini et al. (2004) reported a well-preserved dinoflagellate cyst assemblage from the Manusela Limestone (previously the Asinepe Limestone) from Indonesia. This area was an island situated between Tethys and Panthalassa during the Late Triassic (Golonka, 2007). Together with abundant terrestrially derived palynofloras, Martini et al. (2004) recorded *Beaumontella caminuspina, Beaumontella delicata*, *Heibergella aculeata, Heibergella asymmetrica* and *Rhaetogonyaulax rhaetica*. They correlated this assemblage to the middle–upper Norian *Heibergella* (now *Hebecysta*) *balmei* Interval Zone (Helby et al., 1987a). This is supported by evidence from corals and foraminifera with a clear Tethyan affinity (Charlton and van Gorsel, 2014). From Seram, Helby et al (1987) reported rare *Sverdrupiella* in association with *Heibergella* in the shallow water Kanikeh Formation. A short paper from the Andaman Islands, India (Sharma and Sarjeant, 1987), reported *Heibergella* spp. and *Rhaetogonyaulax rhaetica,* and linked these observations to Indonesia.

There is only one record of Triassic dinoflagellate cysts from Antarctica. Foster et al. (1994) reported and illustrated one specimen of *Rhaetogonyaulax* from the Flagstone Bench Formation of East Antarctica. This co-occurs with a well-preserved terrestrial Onslow Microflora of Norian age. No other independent dating was available.

2.5. Africa

From the Upper Triassic Mbuo Formation in southern Tanzania, Hudson and Nicholas (2014) reported *Dapcodinium priscum, Sverdrupiella* sp. and *Sahulidinium ottii* from explorations wells. However, they based their observations on unpublished industry reports and their only general age assignment is correlation of the terrestrial and marine palynomorph assemblages.

2.6. South America

No records of Late Triassic dinoflagellate cysts from South America have been reported thus far. Most of the known successions are non-marine, for example the Ischigualasto Formation of Argentina. Nonetheless, Upper Triassic marine successions are known, for example, in Mendoza Province of central western Argentina, where Norian–Rhaetian bivalves and brachiopods were reported by Damborenea and Manceñido (2012) and Damborenea et al. (2017). Furthermore, Sansom (2000) documented Rhaetian conodonts and ichthyoliths from Chile, and Ferrari (2015) reported Rhaetian marine gastropods from Peru, but relatively little palynological research has been done on the fragmentary and sparse Upper Triassic strata along this margin.

3. The stratigraphic records of Triassic dinoflagellate cysts

3.1. Upper Ladinian? to Lower Carnian

To date, the first known fossil dinoflagellate cysts recorded are *Sahulidinium ottii* from the upper middle Triassic/lowermost Carnian of Australia, however the dating is uncertain and is based on indirect evidence (Riding et al., 2010). Following substantial hiatuses representing a time interval with no records of about 10 my, the next published occurrences from this area are those from the upper Carnian. However, small *Rhaetogonyaulax* have been recently recorded in lower Carnian successions from Australia (personal communication, Daniel Mantle 2018), indicating this the apparent gap may actually represent a continuous record. Stratigraphically, the next published occurrences on a global scale are those from the northern shores of the Neotethys. These includes the lower Carnian occurrences of Switzerland (Stover and Helby, 1987; Hochuli and Frank, 2000) and Hungary (Baryani 2018). The two latter records are geographically separated and stratigraphically isolated, but were connected to the Neotethys, an area with carbonate platforms and reefs. The reported species includes *Rhaetogonyaulax* cf. *wigginsii*, an "Australian" species, cf. *Noricysta* (Switzerland) and *Heibergella* sp. (Hungary). Interestingly none of these taxa have so far been recorded in the Carnian from the northern shores of Pangea.

3.2. Upper Carnian

Although records of Late Triassic dinoflagellate cysts from Pangea are fragmentary and sporadic, and they are likely under-reported, dinoflagellate cysts seem to appear relatively synchronously and consistently around Pangea from near the base of the upper Carnian (Figure 2). In all areas, *Rhaetogonyaulax* seems to have been the pioneer genus.

In Australia, *Rhaetogonyaulax wigginsii* has been recorded from the upper Carnian (Stover and Helby, 1987; Riding et al., 2010) and, with the exception of *Suessia swabiana,* no other pre-Norian taxa are apparently present in this area. There are no confirmed records of *Suessia swabiana* until the Rhaetian in other areas, but *Suessia* sp. cf. *Suessia swabiana* was reported by Suneby and Hills (1988) from the Norian in the Sverdrup Basin.

Along the northern shores of Pangea, *Rhaetogonyaulax arctica* was the first species to appear. So far, records include those from the embayment comprising the Norwegian Arctic (Vigran et al., 2014; Paterson and Mangerud, 2015), the Sverdrup Basin (Fisher and Bujak, 1975; Bujak and Fisher, 1976, Felix and Burbridge 1978) and Alaska (Wiggins, 1973), an area facing the open Panthalassa Ocean.

There is still some uncertainty related to the occurrences of other species in the upper Carnian, as there are published records of other taxa from the upper Carnian in the Sverdrup Basin. However, these richer Carnian records are from ditch cuttings samples (e.g. Bujak and

Fisher 1976, table 1 for the Skybattle Bay-15 well below 7594 feet) and it is therefore possible that these occurrences represent caving from the overlying Norian shales. In the Barents Sea, the only record of possible pre-Norian taxa other than *Rhaetogonyaulax* species are those of Hochuli et al. (1989). These authors reported *Heibergella asymmetrica, Heibergella salebrosacea* and *Sverdrupiella mutabilis,* co-occurring with *Rhaetogonyaulax arctica,* in their Assemblage C which they assigned an early Norian age. Paterson and Mangerud (2015) however, did not record these species on Hopen. Vigran et al. (2014), recorded similar assemblages from the Knorringfjellet Formation of Norian age in the Festningen section. Only species of *Rhaetogonyaulax* were recorded below the base of the Norian at this locality. As Hochuli et al. (1989) do not provide range charts from the various localities, there is still uncertainty as to the first appearance of these species. Neither can we rule out that the appearance of *Rhaetogonyaulax* is diachronous across the region due to the flooding from the Northwest. Nonetheless, it seems clear that *Rhaetogonyaulax* was the pioneer genus, but that different species of this genus appeared approximately simultaneously on the northern and southern flanks of Pangea. If this hypothesis is correct, it implies that the number of pre-Norian forms globally were probably between three and five species. No earlier records have so far been published from these localities, despite the fact that Middle Triassic successions in these regions are dominantly marine, and have yielded many acritarchs.

3.3. Norian

Although relatively few marine Norian successions which have produced dinoflagellate cysts have been observed on a global scale, several of them comprise relatively diverse and rich assemblages. This Norian “explosion” appears to be a genuine evolutionary event and its inception in the northern areas coincided with a major transgression where ammonoids provide independent dating for some of the palynological records. However, the general scarcity of independent age control, later changes in lithostratigraphical successions, uncertainties as to stage boundaries and stage durations, and thereby ties to the time scale, makes it difficult to distinguish early and late Norian dinoflagellate cyst assemblages. However, it seems clear that early Norian records include those from northern Pangea (Alaska, the Barents Sea and the Sverdrup Basin) and from Australia, which was located on the southern shores facing the Neotethys. Additionally, there are reports from Iran, which was located in the northern parts of the Neotethys (Figure 2). The age constraints for these are relatively good; several of these sections have independent ammonite control.

The dinoflagellate cyst assemblages reported as of early Norian age from the Sverdrup Basin in the Canadian Arctic, included *Valvaeodinium* (as *Comparodinium*) and *Suessia* sp. cf. *S. swabiana* (see Suneby and Hills 1988). Theses authors also reported upper Norian assemblages comprising *Noricysta pannucea* and *Heibergella asymmetrica*. Other records were given a general Norian age including those of *Hebecysta brevicornuta*, *Heibergella aculeata*, *Noricysta fimbriata*, *Noricysta varivallata*, *Sverdrupiella mutabilis*, *Sverdrupiella sabinensis* and *Sverdrupiella septentrionalis*. Suneby and Hills (1988) also reported undifferentiated forms of *Rhaetogonyaulax* and Fisher and Bujak (1975) and Bujak and Fisher (1976) recorded various species of *Hebecysta, Heibergella, Noricysta* and *Sverdrupiella* from the western Queen Elisabeth Islands.

In contrast to the diverse associations from the Sverdrup Basin, mainly *Rhaetogonyaulax arctica* and *Rhaetogonyaulax rhaetica* are present in the lower Norian of the Norwegian Arctic, although *Heibergella*, *Noricysta* and *Sverdrupiella* occur rarely (Vigran et al., 2014; Paterson & Mangerud, 2015). This could be due to the fact that the Barents Sea was situated in the inner part of a huge embayment which received massive levels of clastic input from the eroding Uralides mountains resulting in a dominantly paralic basin fill, with occasional marine incursions. The largest of these was the early Norian transgression. The upper Norian in the Norwegian Arctic is devoid of marine palynomorphs.

In the Neotethys area, Norian dinoflagellate cyst records are so far restricted to Iran (Aghanabati et al. 2002; Aghanabati et al. 2004; Ghasemi-Nejad et al., 2004). From northern Iran the lower middle Norian dinoflagellate assemblages are relatively rich comprising abundant *Rhaetogonyaulax wigginsii*, *Heibergella asymmetrica*, *Heibergella salebrosacea* and *Heibergella aculeata* (see Ghasemi-Nejad et al. 2004), resembling the assemblages from Australia. Above in the Iranian successions, Ghasemi-Nejad et al. (2004) only recorded species of *Rhaetogonyaulax* including *Rhaetogonyaulax rhaetica,* which they assigned a younger late Norian to Rhaetian age. Also in Indonesia *Rhaetogonyaulax rhaetica* was reported as of middle–late Norian age. It therefore seems that *Rhaetogonyaulax rhaetica* appeared later in the Neotethys area compared to the northern flanks of Pangea, where it appears in the early Norian. In northeastern Iran, Ghasemi-Nejad et al. (2008) also recorded *Sverdrupiella* in assemblages of early Late Norian age. As no independent age control is available here, it is, however, difficult to correlate this more exactly to other areas than anticipating a general Norian age.

From Indonesia, situated latitudinally between Iran and Australia, Martini et al. (2004) recorded similar Norian assemblages; however, they also reported *Beaumontella caminuspina,* and *Beaumontella delicata*. This is interesting as *Beaumontella* was previously considered to have its first global appearance in the Rhaetian, for example *Beaumontella langii* from the Rhaetian of England and in the uppermost Rhaetian in Australia (Bucefalo Palliani and Buratti, 2006; Riding et al., 2010). Interestingly *Beaumontella langii* has, recently also been recorded from the late Norian in Australia (personal communication Daniel Mantle, 2018) showing that *Beaumontella* most likely appeared in the Neotethyan area and migrated when the rifting increased.

In Australia, *Rhaetogonyaulax wigginsii* appeared around the Carnian–Norian transition (see above). In addition to *Rhaetogonyaulax wigginsii*, *Wanneria listeri* has a first appearance in the lowermost Norian. These first occurrences are therefore distinctly different from the those on the northern flank of Pangea. In Australia, these species are followed by *Hebecysta balmei, Noricysta* spp. and *Sverdrupiella* spp., resembling the assemblages in the Sverdrup Basin at the generic level. Also from the Carnarvon Basin, Backhouse et al. (2002) reported upper Norian dinoflagellate cyst assemblages dominated by *Hebecysta balmei* occurring in relatively thin intervals linked to flooding events.

The *Sverdrupiella* suite had a circum-Pacific distribution during the Norian, according to Helby et al. (1987b). The species in the high northerly latitudes are, however, different from those from Australia (Helby and Wilson, 1988) where *Sverdrupiella* appear to be rare. *Sverdrupiella* sp. cf. *S. septentrionalis* and *Sverdrupiella* cf. *S. mutabilis* are recorded from Iran, and rare *Sverdrupiella usitata* from Australia (Backhouse et al., 2002). Helby and Wilson (1988) described *Sverdrupiella warepaensis* from New Zealand. Other Australian records have reported undifferentiated *Sverdrupiella* spp. (Riding et al., 2010). With the exception of *Sverdrupiella warepaensis,* species of *Sverdrupiella* are few in Australia. The rich *Sverdrupiella* suite is mainly confined to the high northerly latitudes; in the Canadian Arctic nine species were recorded. The majority of the Arctic records outside the Sverdrup Basin include sparse occurrences from Alaska and the Barents Sea, most are only identified at the generic level. One of us (JBR) has observed the entire *Sverdrupiella* suite from the Northern Slope of Alaska (unpublished data), but there are large regions of this state where this flora is apparently absent (personal communication, Robert Ravn). *Sverdrupiella usitata* is typically the most common species of this assemblage, and has been observed reworked into younger strata (unpublished data). Based on the published records reviewed in the present account the number of dinoflagellate species had globally exceeded 25 by the end of the Norian–Rhaetian transition.

3.4. *Rhaetian*

During the Rhaetian, marine inundation of the gradually opening rift system led to the expansion of habitats for dinoflagellates. The Rhaetian transgression resulted in dinoflagellate cyst migration into formerly land-locked regions of northern Pangea, including Austria, Denmark, England, France, Italy, Slovakia, Sweden and Switzerland. In addition, there are a number of Rhaetian records from other Neotethyan localities including Australia, Ciscaucasia and east central Iran. In contrast to the Tethyan occurrences, the localities from the northern shores of Pangea are characterised by paralic facies resulting in mainly non-marine Rhaetian successions in the Barents Sea area and the Sverdrup Basin.

The Rhaetian assemblages are somewhat different to their Carnian and Norian counterparts, with *Dapcodinium priscum* having its lowermost occurrence over a wide area. The other dinoflagellate cyst genus expanding in the Rhaetian is *Wanneria*, which first appears in Australia and seems to have migrated northwards. *Wanneria misolensis* has a short range in the early Rhaetian in Australia and is a useful marker. The cosmopolitan species *Rhaetogonyaulax rhaetica,* which first appeared in the late Carnian, expanded both in numbers and spatial extent during the Rhaetian and apparently became extinct close to the Triassic–Jurassic boundary. Most other Triassic genera also extended into the Rhaetian and had range tops close to the Triassic -Jurassic boundary. An exception to this is *Sverdrupiella*, which is extremely rare in the Rhaetian. This genus was reported from the Rhaetian in Europe by Morbey and Dunay (1978) and Powell (1992); however, these authors did not document where *Sverdrupiella* was recorded or provided illustrations. The latter report is of a single specimen of *Sverdrupiella* sp. from the Rhaetian of the Blyborough Borehole, Lincolnshire, central England (JBR unpublished information).

A global regression caused an extremely widespread hiatus near the end of the Triassic; however, a late Rhaetian transgression has been recognised in several areas. This frequently resulted in an influx of dinoflagellate cysts. In southern Sweden, Lindström and Erlström (2006) recorded the suessiacean species *Lunnomidinium scaniense*, together with *Rhaetogonyaulax rhaetica,* below an influx of *Rhaetogonyaulax rhaetica*, with *Dapcodinium priscum* just below the Triassic–Jurassic boundary. This represents the maximum extent of the Rhaetian sea in this area.

A detailed analysis of the Triassic–Jurassic boundary is beyond the scope of this paper. However, we note that there are uncertainties due to condensed sections and hiatuses in the Global Stratotype Section and Point (GSSP) for the Hettangian at Kuhjoch, Austria (Morton, 2012; Hillebrandt et al., 2013). Important studies on the palynology of the Triassic–Jurassic boundary include Kuhjoch (Kürschner et al., 2007; Bonis et al., 2009), St. Audrie's Bay, UK (Bonis et al. 2010), and the Danish/Swedish basins (Lindström and Erlström, 2006; Lindström et al., 2017a,b). Of the main Triassic dinoflagellate cyst taxa, only *Beaumontella langii, Dapcodinium priscum* and *Heibergella*? *kendelbachia* extended into the Jurassic (Figure 2).

4. The paleoenvironmental preferences of Triassic dinoflagellate cysts

At present, knowledge concerning the paleoenvironmental preferences of Late Triassic dinoflagellates is very limited, and no focussed studies on this topic have been performed. In most cases, their use as marine indicators have been their most important input. There are occasional observations on their link to depositional environments for example, Helby et al (1987) noted that *Sverdrupiella* on the Alaskan shelf was recorded in clastic sediments with high nutrient contents and restricted circulation. However, there are at present insufficient data to draw conclusions on this point.

One of the few attempts to link upper Triassic dinoflagellate cysts to paleoenvironmental conditions include Courtinat and Piriou (2002) who recorded *Dapcodinium* and *Rhaetogonyaulax* from the Rhaetian of the Tethyan region, frequently in an inverse quantitative relationship. Batten et al. (1994) and Poulsen (1996) have also noted this configuration. Courtinat and Piriou (2002) related this phenomenon to a mainly restricted nearshore marine versus a deeper marine environment. They noted that *Rhaetogonyaulax rhaetica* seemed to occur in more marine settings, compared to *Dapcodinium priscum* which was recorded in more restricted depositional settings. They postulated that *Dapcodinium* is therefore probably a more opportunistic euryhaline species. By contrast, Batten et al. (1994) suggested that *Rhaetogonyaulax rhaetica* may have been more tolerant of brackish water conditions, as it occurs in marine mudstones close to an intra-basinal high in the Danish Basin. In their study *Dapcodinium priscum* was recorded with well-preserved plant material. Ghasemi-Nejad et al. (2004) in more general terms related their dinoflagellate records to a shallow sea with fluvial deposition, leading to rich nutrient conditions as a cause for dinoflagellate cysts to flourish.

Rhaetogonyaulax rhaetica has been recorded in the terrestrially-dominated, shallow marine successions for example of Slovakia (Ruckwied and Götz, 2009) in relatively low proportions. Most records of *Rhaetogonyaulax* appear however to represent relatively deeper water environments such as outer shelf. Paterson et al. (2016) demonstrated that *Rhaetogonyaulax rhaetica* had abundance peaks which correlate to maximum flooding surfaces. From the same study, *Rhaetogonyaulax arctica* seemed to occur during the early stages of transgression (Paterson & Mangerud 2014, Paterson et al. 2016). The palaeoenvironmental significance of this genus is therefore not fully understood. As more dinoflagellate cyst data become available from the Upper Triassic, there should be potential to link them to depositional settings and potentially use them as paleoenvironmental proxies.

5. Conclusions

Based on present knowledge from published records, this review has shown that the global appearance of dinoflagellate cysts around the shores of Pangea took place near the base of the Upper Triassic, maybe as early as in the latest Middle Triassic in Australia. This marks the first appearance of a new group of marine plankton in the oceans. The peridiniphycidaen genus *Rhaetogonyaulax* seems to be the pioneer in all areas, and the cosmopolitan species *Rhaetogonyaulax rhaetica,* which first occurred in the late Carnian, expanded in both numbers and spatial extent during the Rhaetian. Four peridiniphycidaen genera (*Hebecysta, Heibergella, Rhaetogonyaulax* and *Sverdrupiella*), and one suessiaceaen genus (*Noricysta)* had already developed globally by the middle Norian on the northern side of Pangea, whereas another two suessiaceaen genera (*Suessia* and *Wanneria*) had developed in the southern shores of Neotethys in Australia. Following these genera, *Valvaeodinium* appeared within the middle part of the Norian, followed by *Beaumontella*. The latter genus was previously thought to be confined to the Rhaetian, but is recorded in upper Norian successions in Australia and Indonesia. Near the base of the Rhaetian, *Dapcodinium* appears for the first time. Many dinoflagellate cyst species are endemic, being confined to the northern or southern realms, and the lack of independent dating makes precise correlation of the various assemblages difficult.

It is clear that most Triassic genera extended into the Rhaetian, but *Sverdrupiella* seems to be an exception, as it is extremely rare in the Rhaetian. The majority of Triassic dinoflagellate cyst taxa became extinct at the Triassic–Jurassic boundary. The exceptions are *Beaumontella langii* and *Dapcodinium priscum,* which range up into the lower Jurassic.

Knowledge on the paleoenvironmental significance of Late Triassic dinoflagellate cysts is so far extremely limited.

Outstanding problems in understanding the spatial and temporal occurrences of Late Triassic dinoflagellate cysts include the lack of records from Russia. Here, the potential for future studies appears high because well-known ammonite dated marine successions are present, and dinoflagellate cysts have been observed (see above). In addition, lack of records from South America and other areas along the eastern side of Pangea hampers for example the understanding of potential migration routes. In order to improve our knowledge on the oldest occurrences of dinoflagellate cysts, studies of frontier areas, combined with more detailed studies from the areas where they are already known to occur, offer rich potential for future studies.

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FIGURES

Figure 1. The palaeogeography of the Late Triassic illustrating the locations of first occurrences of dinoflagellate cyst records (adapted from Golonka et al. 2018).

Figure 2. A composite range chart of Late Triassic dinoflagellate cysts from various geographical areas (time scale from Gradstein et al. 2016).

TABLE 1

List of dinoflagellate cyst taxa appearing in Upper Triassic successions. References to the author citations can be found in Williams et al. (2017).